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Pseudotrismegistia H. Akiy. & Tsubota, a New Genus of the Sematophyllaceae (Musci)

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A new monotypic genus, *Pseudotrismegistia* H. Akiy. & Tsubota, is proposed to accommodate *P. undulata* (Broth. & Yasuda) H. Akiy. & Tsubota. *Pseudotrismegistia* differs from the widely distributed genus *Trismegistia* in the weak differentiation of leaf shape between stems and branches, strong undulation in the upper portion of the leaf lamina, clearly differentiated forked costae of leaves, absence of well-marked borders at the leaf margins, and the alar cells arranged in a scalariform manner. The nearly equal size of alar cells that are scarcely inflated, as well as molecular analyses, suggests the genus should be assigned to the Heterophylliideae of the Sematophyllaceae.

Key words: *Mastopoma*, *Pseudotrismegistia*, *rbc*L, Sematophyllaceae, *Trismegistia*,

The genus *Trismegistia* (Muell. Hal.) Muell. Hal. (type species: *Trismegistia complanatula* (Muell. Hal.) Muell. Hal. in Broth.) is a member of the Sematophyllaceae and over fifty taxa have been described, most of them distributed in the tropical Asia and Oceania (Wijk *et al.* 1969). Several species have been reported from other continents, but they have been transferred to other genera, such as *Heterophyllium* and *Wijkia*. In the course of taxonomic revision of the *Trismegistia*, the senior author has recognized that there are several taxa wrongly placed in the genus. Although most of them will be treated in a separate paper, here we propose a new genus to accomodate *Trismegistia undulata* Broth. & Yasuda and *T. perundulata* Dixon along with taxonomic discussion on *Trismegistia* and related genera.

Pseudotrismegistia H.Akiy. & Tsubota **gen. nov.** (Sematophyllaceae)

Affinis *Trismegistiae*, sed foliis caulibus et ramis haud diversis, ligulatis et undulatis superne, cellulis marginalibus haud incrassatis, limbis destitutis, costis foliibus praesentibus furcatis, cellulis alaribus scalariformibus haud inflatis diversa.

Type. Pseudotrismegistia undulata (Broth. & Yasuda) H. Akiy. & Tsubota

Plants green when fresh, more or less shiny, pinnately branched, procumbent on substrata or somewhat pendent, rarely obliquely upright. Stipes usually absent (rarely developed when growing on rotten logs or boulders). Stem leaves larger than branch leaves, but similar in shape. Branch leaves lanceolate, more or less narrowed at the shoulders into ligulate upper portions, distinctly undulate above; margins entire and sometimes incurved below, densely serrate in upper 2/3; costa clearly differentiated, short and double, or forked. Alar cells not inflated and arranged in scalariform, almost equal size. Lamina cells linear-fusiform, scarcely pitted, not differentiated at margins. Perichaetia developed on stems. Perichaetial leaves triangular, narrowed into long, slender apices, incurved below, plane and serrulate above, deeply plicate, alar region not differentiated; costa indistinct; vaginular hairs sparse. Perigonia and calyptrae unknown.

Pseudotrismegistia undulata (Broth. & Yasuda) H. Akiy. & Tsubota, **comb. nov.** (Figs. 1 - 20; Map 1)

Basionym: *Trismegistia undulata* Broth. & Yasuda in Broth., Rev. Bryol. 53: 4 (1926).

Type. FORMOSA, Mt. Daibu, Nov. 20, 1918, *E. Matsuda 608* (Holotype H-BR:ref. no. 43210009)

Synonym. *Trismegistia perundulata* Dixon, Ann. Bryol. 9: 69 (1936) = *Mastopoma perundulatum* (Dixon) Horik. & Ando, Nature and Life Southeast Asia 3:34 (1964).

Type. LAOS, Zchiengkwang, Pu Bia, *Kerr 515* (Holotype BM).

Plants to 15 cm long, pinnately branched, usually procumbent on tree trunks, sometimes bearing obliquely ascending stems when growing on fallen logs or boulders. Stem leaves linear lanceolate (Taiwan and China plants) or widely ovate below, abruptly narrowed at shoulder into ligulate upper lamina (Laos and Thailand plants), to 4 mm long, strongly undulate in upper portions, more or less concave below; margins entire and often incurved below, sharply serrate above; costa short, to 1/5 of leaf length, double or unevenly forked; lamina cells fusiform to linear, pitted or scarcely pitted, not differentiated at margins; alar cells scalariform, in 6 - 7 rows and tiers, not inflated, pale yellow. Branch leaves to 2.8 mm long, similar to stem leaves in shape, less undulate.

Setae 5 - 6 cm long, smooth, reddish brown, becoming blackish when aged. Capsules ovoid, to 2.5 mm long, inclined to somewhat pendent, reddish brown, smooth; exothecial cells quadrate, slightly collenchymatous with rounded corners; stomata present. Opercula conical, with short rostrum. Peristome white to pale yellowish brown, double, alternately arranged. Exostome teeth 16, linear lanceolate, 600 - 700 µm long, finely and transversely striate, papillose only on the distal portions. Endostome segments linear lanceolate, papillose throughout, equal in length to exostome teeth; cilia 2 - 3, often connate or lacking; basal membranes high, about 1/2 of segment in length. Spores spherical, finely papillose, 15 - 23 µm in diameter.

Habitat. On tree trunks, sometimes on rotten logs and boulders covered by other bryophytes, in mossy and elfin forests over 1800 m in altitude.

Distribution. Laos, northern Thailand, China, and Taiwan.

Specimens examined. **LAOS**: holotype (BM). **THAILAND**. **Chiangmai Co**.: Doi Inthanon, 2550 m, *Akiyama Th-1*, *Th-35* (HYO; both with sporophytes); ibid., 2160 m, *Akiyama Th-81*, *Th-88*, *Th-101* (HYO; all with sporophytes); ibid., *van Beusekom B234* (L, with sporophytes); ibid., 2600 m, *Yoda 137*, *140* (HIRO); ibid., 2000-2300 m, *Umesao 65* (HIRO); ibid., 2300-2600 m, *Yoda 76*, *78*, *86*, *95*, *101*, *113*, *138* (HIRO); ibid., 2400-2600 m, *Geesink 8404*, *8409* (with sporophytes), *8427* (L). **CHINA. Hainan Co**.: second peak Wuzhi Mt., 1800 m, *1977 Collecting Team 2350* (FH). **TAIWAN**. **Taichung Co**.: Mt. Hassen, 7000 - 8000 ft., Aug. 15, 1928, *Aoki s.n.* (Taiwan University Herbarium, TNS). **Jiayi Co**., Mt. Arisan, Dec. 28, 1913, *Ara s.n.* (Taiwan University Herbarium, TNS). **Pintou Co**., Shei-Pa National Park, Mt. Peitawu (= Mt. Defu or Mt. Daibu), in the vicinity of Hinokidani-sanso

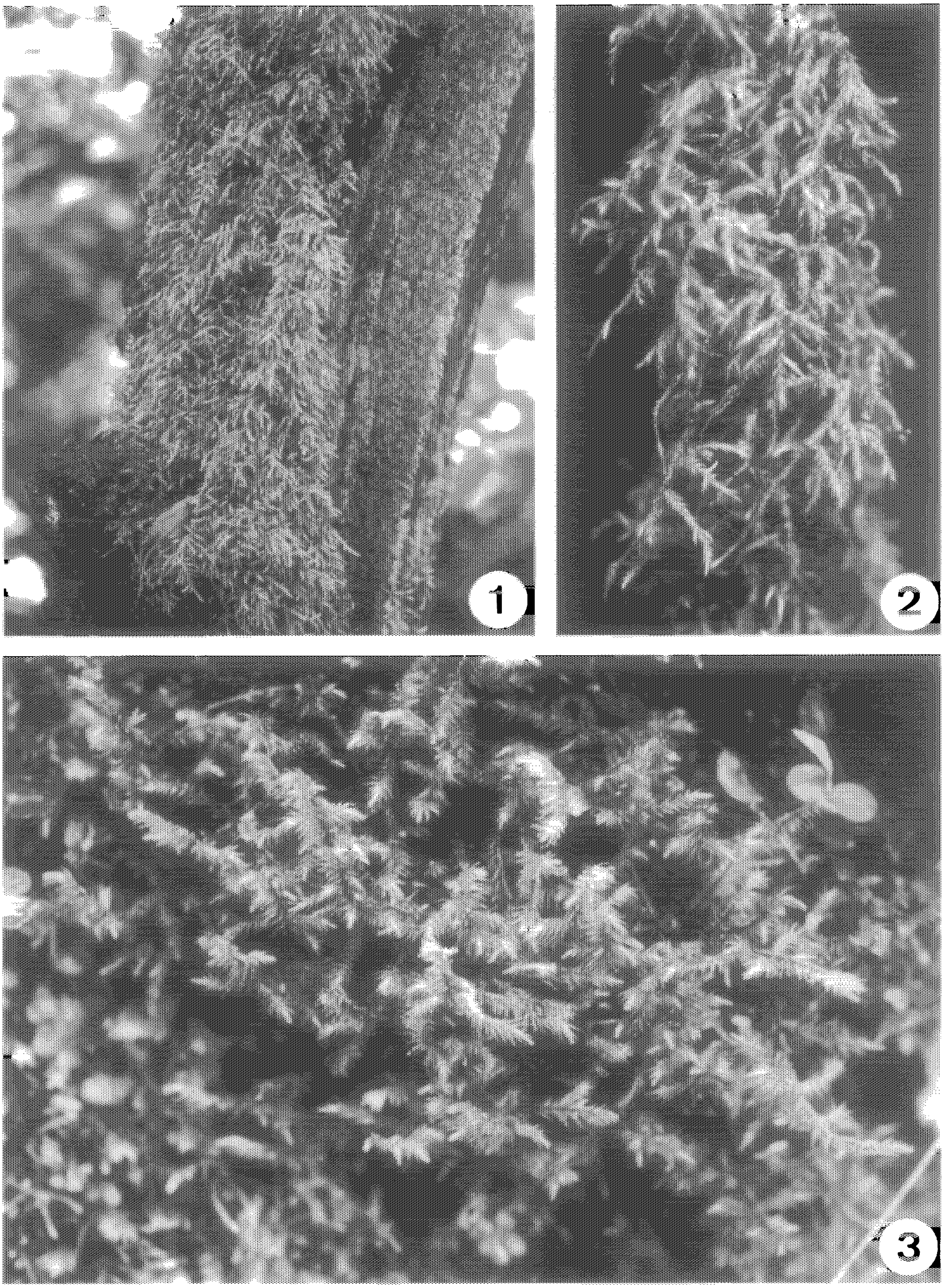


FIG. 1-3. Photographs of *Pseudotrismegistia undulata*. 1: Habitat (Thailand; *Akiyama Th-1*). 2: Plant with sporophytes (Thailand; *Akiyama Th-1*). 3: Plant of Taiwan population (Taiwan; *Akiyama et al. 67*).

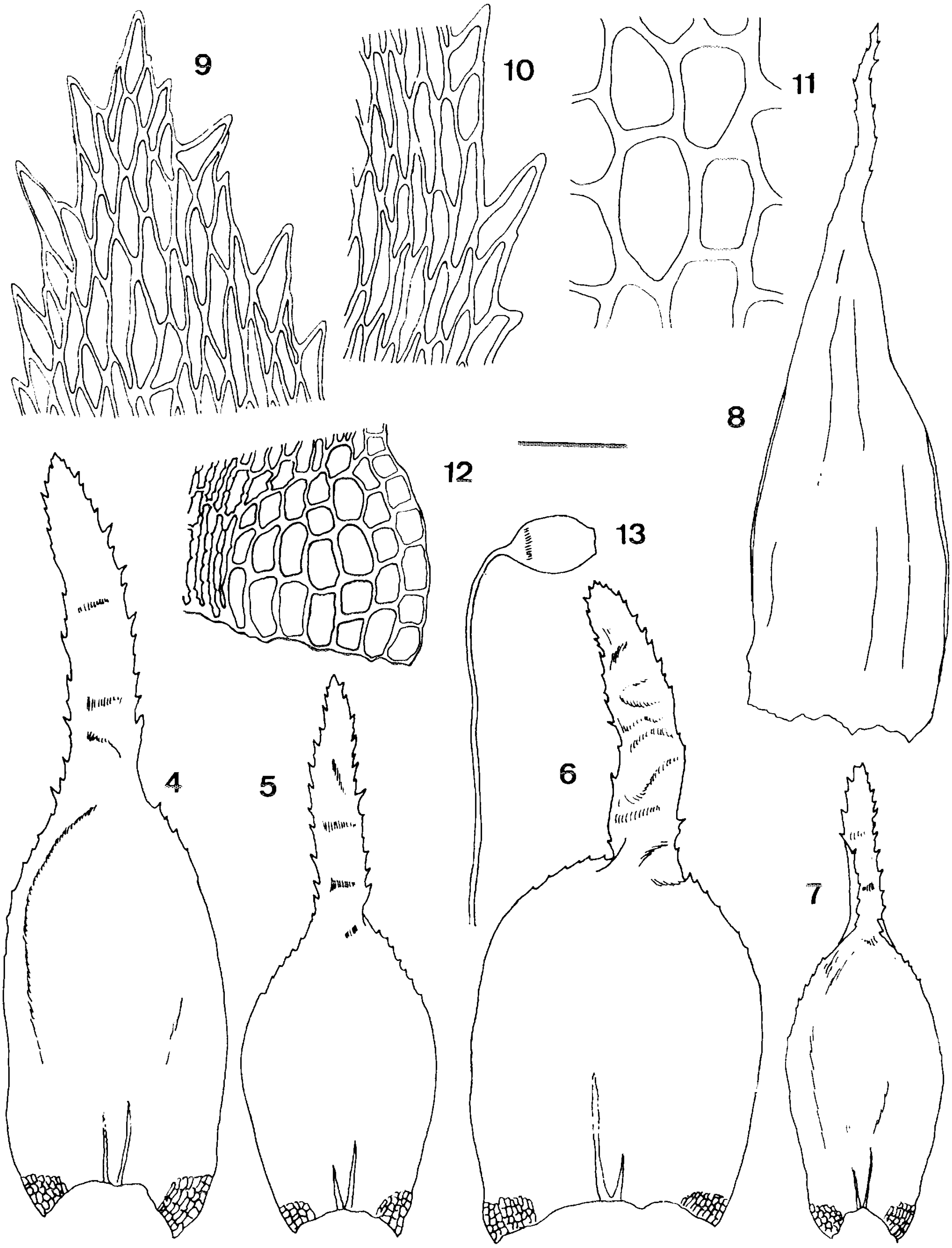


FIG. 4-13. *Pseudotrismegistia undulata* (Laos and Thailand plants). 4 and 6: stem leaves. 5 and 7: branch leaves. 8: perichaetial leaf. 9: apex of stem leaf. 10: upper margin of stem leaf. 11: exothecial cells of capsule. 12: alar region of stem leaf. 13: sporophyte. Scale bar: 0.5 mm for 4 - 8; 0.05 mm for 9 - 11; 0.1 mm for 12; 2 mm for 13. 4 -5 & 13: *Akiyama et al. 67* (HYO). 6 - 12; *Kerr 515* (holotype, BM).

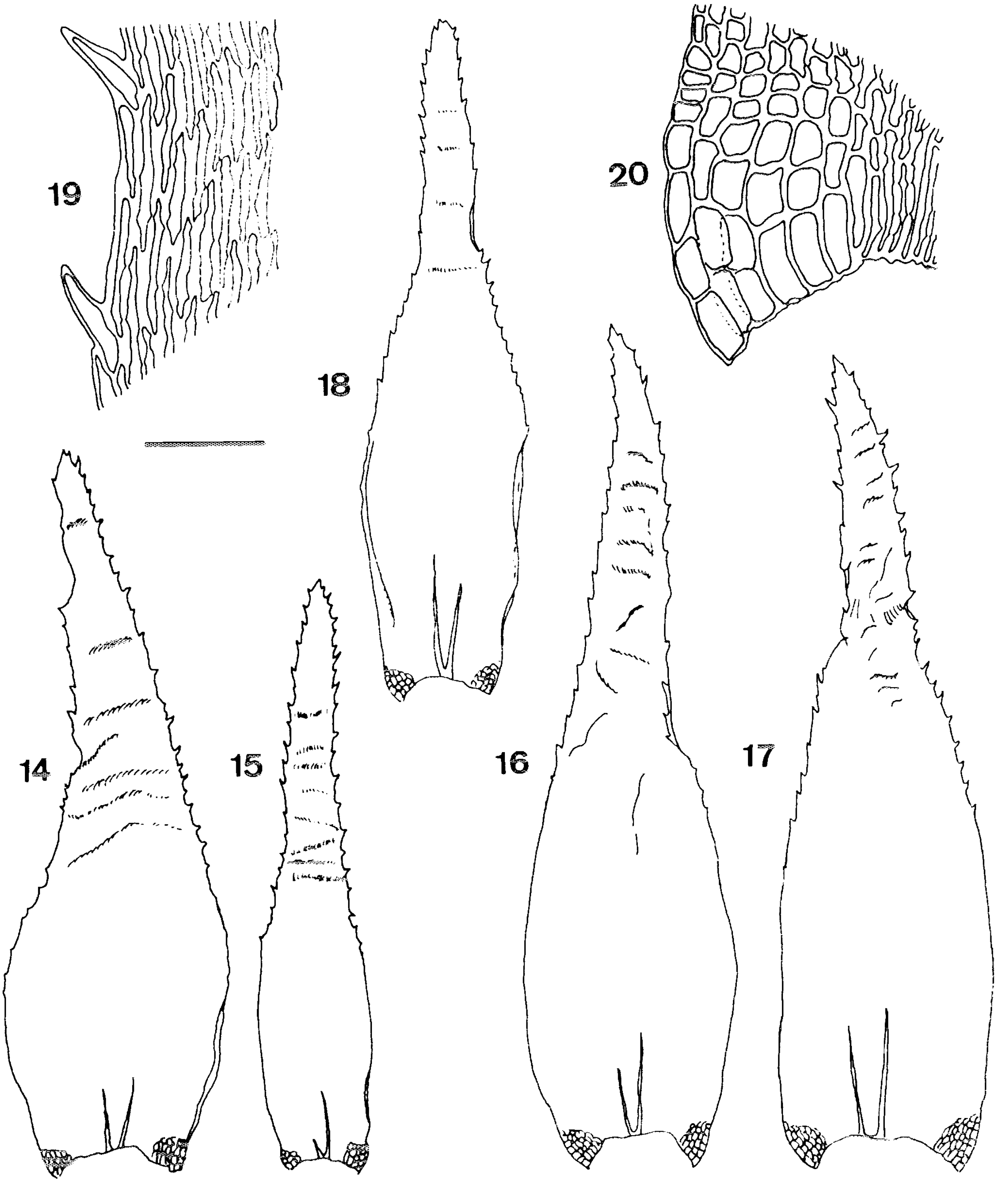


FIG. 14-20. *Pseudotrismegistia undulata* (Taiwan and China plants). 14, 16, 17, and 18: stem leaves. 15: branch leaf. 19: upper margin of stem leaf. 20: alar region of stem leaf. Scale bar: 0.5 mm for 14 - 18; 0.05 mm for 19; 0.1 mm for 20. 14, 15, 19, and 20: *Matsuda s.n.*, Nov. 20, 1918 (holotype, H-BR). 16: *Aoki s.n.*, July 25, 1985 (TNS). 17: *Akiyama T-67* (HYO). 18: *1977 Collecting Team 2350* (FH).

mountain villa, ca. 2000 m, *Akiyama et al. 67* (HYO, HIRO); ibid., Kwaiku to Mt. Peitawu (=Mt. Defu), 2190 - 3090 m, *C.-C. Chuang 1556a* (FH).

Note. In the course of a taxonomic revision of the genus *Trismegistia*, we recognized that the alar organization of *Pseudotrismegistia undulata* differed from that found in *Trismegistia* species:

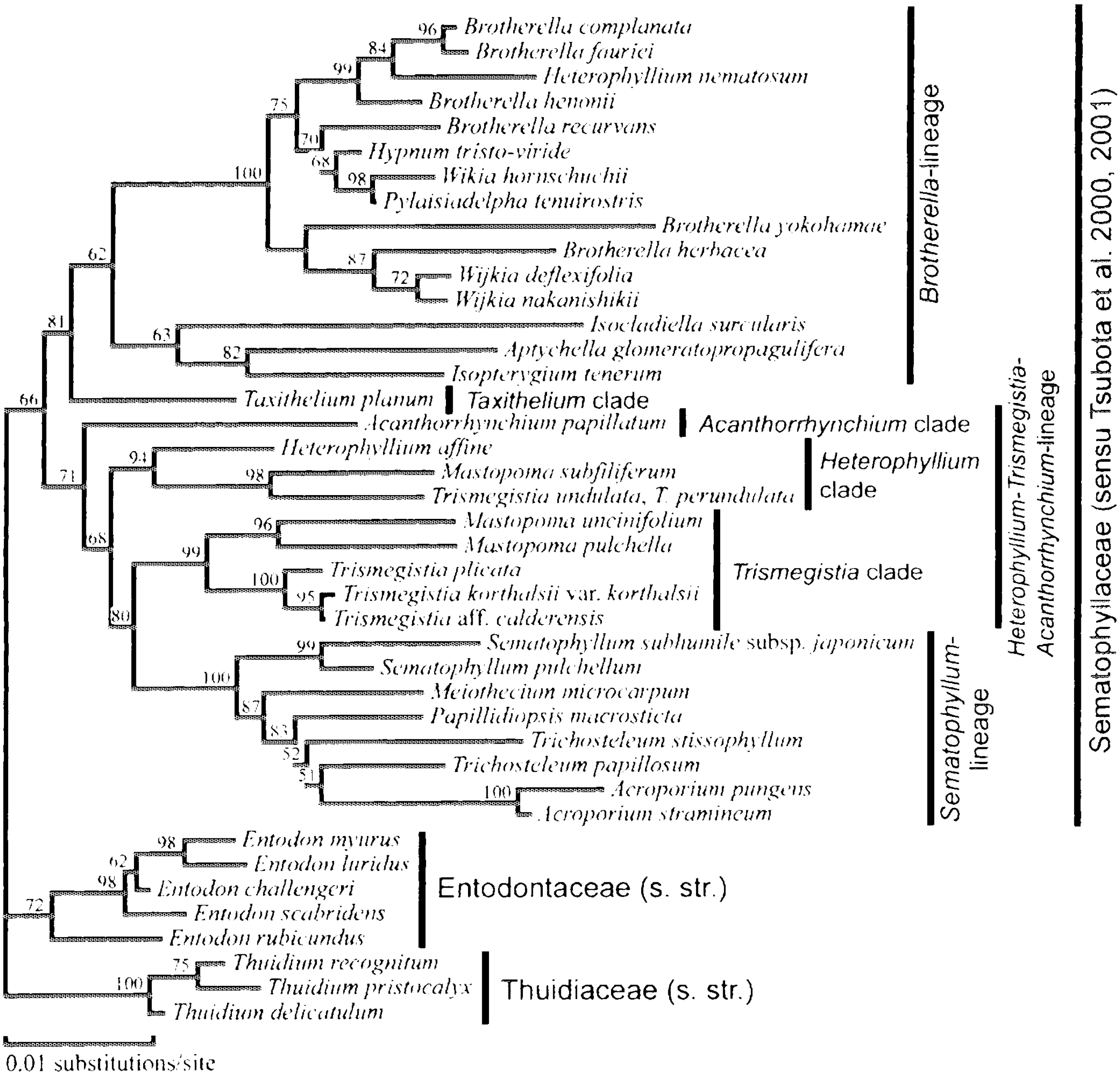
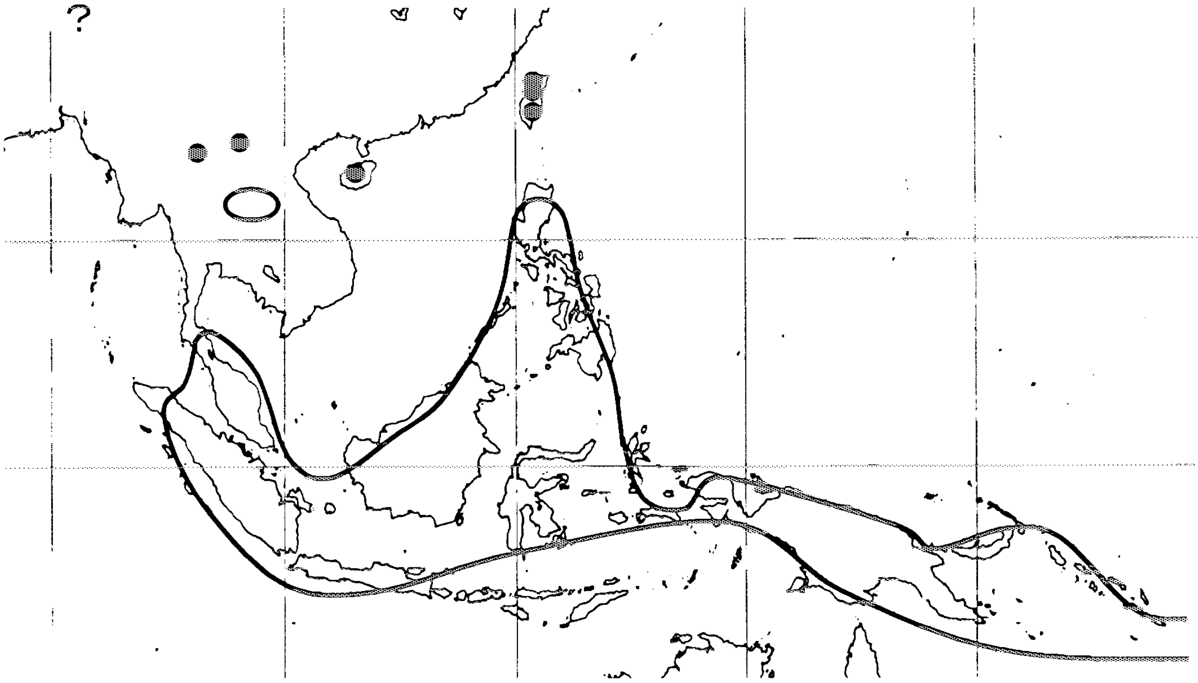


FIG. 21. ML tree of the sematophyllaceous *rbc*L gene sequences (HKY85 model;$\alpha/\beta = 9.59$; ln L = -5213.7 ± 215.7 by NucML) and clades. The horizontal length of each branch is proportional to the estimated number of nucleotide substitutions. The root is arbitrarily placed on the branch leading to the Thuidiaceae (s. str.). Local bootstrap probabilities (%) more than 50% are shown above branches. *Brotherella*-lineage means *Brotherella-Pylaisiadelpha-Wijkia-Isocladiella-Aptychella* clade and *Sematophyllum*-lineage = *Sematophyllum-Acroporium-Meiothecium-Trichosteleum-Papillidiopsis* clade. *Heterophyllium* clade means the *Heterophyllium affine-Mastopoma subfiliferum-Trismegistia undulata-T. perundulata* clade, and *Trismegistia* clade = *Trismegistia korthalsii* var. *korthalsii-T.* aff. *calderensis-T. plicata-Mastopoma uncinifolium-M. pulchella* clade. *Heterophyllium-Trismegistia-Acanthorrhynchium-lineage* unites with *Heterophyllium* clade, *Trismegistia* clade and *Acanthorrhynchium* clade. Sematophyllaceae (*sensu* Tsubota *et al.* 2000, 2001) clade unites with *Brotherella*-lineage, *Sematophyllum*-lineage. *Heterophyllium-Trismegistia-Acanthorrhynchium*-lineage and *Taxithelium* clade. *Trismegisita pulchella* Herz. is shown here as *Mastopoma pulchella*, and the new combination will be published in a separate paper. (Reproduced from Tsubota *et al.* 2001b)

In *Trismegistia*, at least the outer 2 - 3 tiers of alar cells are thin-walled and bulging, and branch leaves often have a single row of alar cells. We regard such a difference as well as the total absence of a leaf border and the undulation of the leaf lamina that is never found in other *Trismegistia* species as sufficient to establish a new genus to accommodate the species. Similar



MAP 1. Distribution of the *Pseudotrismegistia* (•) and *Trismegistia*. Distribution area of *Trismegistia* is shown by a solid line except a single locality at Phu Luang, Northeast Thailand (shown by a circle).

alar organization can be found in the genera *Heterophyllium* and *Gammiella* (subfamily Heterophyllioideae, *sensu* Tan & Buck 1989).

Some members of the Sematophyllaceae - *Trismegistia*, *Mastopoma*, and *Wijkia* (subfamily Sematophylloideae, *sense* Tan & Buck 1989) - have more or less serrate or crenulate leaf margins, and long setae, as in *Pseudotrismegistia*. Tan & Buck (1989) pointed out that members of the Heterophyllioideae can be distinguished from those of the Sematophylloideae by their scalariform alar regions and non-collenchymatous exothecial cells. It is interesting that our new genus *Pseudotrismegistia* shows intermediate characteristics between the two subfamilies, i.e., it possesses scalariform alar regions and collenchymatous exothecial cells. From the molecular phylogenetic results shown below, however, we tentatively include *Pseudo-trismegistia* in the Heterophyllioideae. The validity of the subfamily Wijkioideae, where *Trismegistia* has been classified (e.g., Hedenäs & Buck 1999), is discussed in a separate paper (Tsubota *et al.* 2001b).

Both Horikawa & Ando (1964) and Tan (1991) pointed out that *Trismegistia perundulata* Dix. [= *Mastopoma perundulata* (Dixon) Horikawa & Ando], which is known from Laos and Thailand, and *Trismegistia undulata* Broth. & Yasuda, reported from Taiwan and China, did not differ in their morphology, and they treated the former as a synonym of the latter. After examining all the specimens including types of both species, and making field observations in Taiwan (type locality of *T. undulata*) and Thailand, the two species can be distinguished from each other by the leaf shape: leaves are broadly ovate below, abruptly narrowed at shoulder into ligulate upper portion in *T. perundulata*, while they are narrowly lanceolate, gradually narrowed into apex in *T.*

undulata. According to our molecular analyses using *rbc*L sequences, however, both species differ from each other only by a single site mutation (Tsubota *et al.* 2001b). This kind of difference of sequences is usually found among the same species in bryophytes (Arikawa & Higuchi 1999). Therefore, here we recognize these two taxa as belonging to the same species.

At Doi Inthanon, in December, at the beginning of the dry season, we found a number of colonies of *Pseudotrismegistia undulata* bearing abundant sporophytes. All sporophytes we observed were already deoperuculate. Based on our field observations, this species usually grows on tree trunks to several meters high (Fig. 1). It sometimes formed colonies on rotten logs on the forest floor, where stipes were somewhat developed and branching was in a palmate manner, as in some species of *Trismegistia* (Fig. 2).

As far as we have examined, no sporophytes or even inflorescences have been found among the specimens collected in Taiwan and China. Since these plants lack any kind of specialized asexual reproductive organs, the manner of reproduction is unknown.

Discussion

1. History of the genus and comparison with related genera

Brotherus (1926) described *Trismegistia undulata* from Taiwan, and it was the first record of the genus in East Asia. Then, Dixon (1936) published a new species, *T. perundulata*, from Laos. Later, in the study of the Thailand moss flora, Horikawa & Ando (1964) reported *T. perundulata* from Doi Inthanon and transferred the species to the genus *Mastopoma* mainly because of its conical, short beaked operculum of the capsules. In addition, they suggested that *T. undulata* and *T. perundulata* belonged to the same species. Tan (1991) examined type specimens of both species and also concluded that they are conspecific. Tan (1991), however, thought that operculum structure to be an unreliable character to separate *Trismegistia* and *Mastopoma* and suggested alar cell organization and the differentiated leaf borders could distinguish the two genera. According to him, *Trismegistia* could be circumscribed by divided alar cells forming multiple or scalariform tiers, while *Mastopoma* (at least the Malesian species) are characterized by a single row of enlarged alar cells. Therefore, he did not transfer *T. undulata* into the *Mastopoma* because the species possesses scalariform alar organization. As for the sporophyte features, *Pseudotrismegistia* is similar to *Trismegistia*. They differ only by the presence of stomata at the neck of the capsules in *P. undulata*, wheras all species of *Trismegistia* lack stomata. In other features of the sporophyte, including peristome structure and composition, these two genera do not differ.

Although we consider alar organization to be useful to separate most species of *Mastopoma* from *Trismegistia*, there exists an exception: *Mastopoma subfiliferum* Horik. & Ando, which grows side by side with *Pseudotrismegistia undulata* at Doi Inthanon, and which has divided, scalariform quadrate to subrectangular alar cells that are all of nearly equal size. This alar feature is characteristic for the subfamily Heterophyllioideae of the Sematophyllaceae (Tan & Buck 1989). We think *M. subfiliferum* should be transferred to *Heterophyllium* or placed in a separate new monotypie genus.

Pseudotrismegistia and the related genera as discussed above, as well as this curious species *Mastopoma subfiliferum*, can be distinguished as follows:

Key to *Pseudotrismegistia* and allied genera

1. Alar cells in a single row, more or less inflated. ······ 2
1. Alar cells scalariform, those of outer one to two rows clearly bulging, or all of nearly equal size. ······ 3
    2. Small plants, often bipinnately branched, usually growing on tree trunks and branches. Leaves often conspicuously curled in dry conditions ······ *Mastopoma*
    2. Plants variable in size, often growing on rotten logs or wet boulders. Main stem prostrate on substrata, pinnately branched. Leaves often abruptly narrowed into slender acumen. ······ *Wijkia*
        3. Alar cells of a basal row larger and inflated. [Leaves of stipe (if present), stem, branch, and branchlet clearly different in their shape and size; rugose, plicate, or plane, but never undulate; margins more or less well-differentiated with thick-walled lamina cells and thus forming a border. Costa absent. Exothecial cells thin-walled, slightly collenchymatous.] ······ *Trismegistia*
        3. Alar cells of nearly equal size, not inflated. ······ 4
            4. Leaves ligulate in the upper portion, distinctly undulate above when dry and moist; margin sharply dentate or serrate, distinctly undulate, not bordered. (Stipe usually absent. Stem and branch leaves not differentiated in shape. Costa present, short, forked. Exothecial cells clearly collenchymatous.) ······ *Pseudotrismegistia*
            4. Leaves gradually narrowed into acumen; margins serrulate to crenulate. ······ 5
                5. Leaves shortly acute; margins only crenulate, plants often with filamentous gemmae. ······ *Gammiella*
                5. Leaves gradually narrowed into a long, slender acumen; upper margins serrulate. ······ 6
                    6. Exothecial cells collenchymatous. Plants growing on tree trunks and branches. Cilia two in number but vestigial. ······ *Mastopoma subfiliferum*
                    6. Exothecial cells not collenchymatous. Plants usually growing on rotten logs, tree trunk base, etc. Cilia usually single, as long as the segments. ······ *Heterophyllium*

2. *Phylogenetic position of the genus* Pseudotrismegistia

Tsubota *et al.* (2001a) showed that *Trismegistia undulata* (= *Pseudotrismegistia undulata*) did not form a monophyletic clade with other *Trismegistia* species. To know the taxnomic position of *Pseudotrismegistia* more definitely, Tsubota *et al.* (2001b) expanded their previous analyses to include *Trismegistia perundulata* (= *P. undulata*) as well as three species of the *Mastopoma*. Two samples of *Pseudotrismegistia* were those shown in the list above: Doi Inthanon, *Akiyama Th-1* (*Trismegistia perundulata*) and Mt. Peitawu, type locality, *Akiyama et al. 67* (*Trismegistia undulata*) . Based on chloroplast ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit (*rbc*L) gene sequences from 63 mosses including species of the genera *Trismegistia*, *Heterophyllium*, *Mastopoma* and *Wijkia*, Tsubota *et* *al.* (2001b) suggested that *Trismegistia* was polyphyletic, and two clades (*T. undulata*-*T. perundulata* and *T. korthalsii* var. *korthalsii*-*T.* aff. *calderensis*-*T. plicata*) were recognized (Fig. 21). The clade of *T. undulata*-*T. perundulata*, which is treated in this paper as a single species in *Pseudotrismegistia*, was placed near *Mastopoma subfiliferum* and *Heterophyllium affine*. We interpret the molecular data as suggesting that the clade be recognized as an independent genus. As for the subfamilial position, we tentatively include the genus in the subfamily Heterophyllioideae, although the phylogenetic tree showed the Heterophyllioideae to be paraphyletic.

Trismegistia undulata and *T. perundulata* differ only in a single site in their sequence data (Tsubota *et. al.* 2001b). Such a small degree of difference in *rbc*L gene sequences has been previously reported as infraspecific sequence variation; for example, *Plagiothecium euryphyllum* (1 base), *P. nemorale* (1 base), *P. denticulatum* (4 bases), *P. neckeroideum* (5 bases), and *Rhytidiadelphus triquetrus* (1 base) (Arikawa & Higuchi 1999). We think molecular data support the synonymy of *T. perundulata* and *T. undulata*. We do not treat them as representing any infraspecific taxa, even though they show difference in leaf morphology.

3. Distributional characteristics of the genus Pseudotrismegistia

The genus *Pseudotrismegistia* (Map 1) has a restricted distribution pattern and seems to have evolved in temperate zones in Asia. It is interesting because the genus *Trismegistia* is a typical member of the Malesian elements that seems to have evolved in tropical, continuously moist environments.

Tan & Yu (1999) reported *Trismegistia undulata* (= *Pseudotrismegistia undulata*) from Hainan Island, China. The known distributional range of the genus includes Taiwan, Hainan, and the northern part of Indochina, areas geographically remotely separated from each other. A similar distribution pattern along the northern edge of the East China Sea is found in several other cases; for example, *Isopterygium propagulifera* Toyama has been collected from Vietnam, Hainan and Taiwan (Akiyama, unpublished data), and *Pinnatella taiwanense* Nog. from Vietnam and Taiwan (Enroth 1994). Though these two species do not show clear morphological differentiation within their distribution areas, as in the case of *Pseudotrismegistia*, their potential genetic diversification warrants investigation.

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